Productivity Is a Poor Predictor of Plant Species Richness


For more than 30 years, the relationship between net primary productivity and species richness has generated intense debate in ecology about the processes regulating local diversity. The original view, which is still widely accepted, holds that the relationship is hump-shaped, with richness first rising and then declining with increasing productivity. Although recent meta-analyses questioned the generality of hump-shaped patterns, these syntheses have been criticized for failing to account for methodological differences among studies. We addressed such concerns by conducting standardized sampling in 48 herbaceous-dominated plant communities on five continents. We found no clear relationship between productivity and fine-scale (meters−2) richness within sites, within regions, or across the globe. Ecologists should focus on fresh, mechanistic approaches to understanding the multivariate links between productivity and richness.

For more than three decades, ecologists have debated the role of primary productivity in regulating plant species richness at fine spatial scales (1, 2). Although some studies have advocated multivariate approaches (3–5), much of the debate remains focused on evidence for a single, general relationship between productivity and richness. This classic productivity-richness relationship (PRR) is hump-shaped, with richness increasing at low to intermediate levels of productivity and decreasing at high productivity (6). The mechanisms invoked to explain the decreasing phase of the PRR in terrestrial plant communities have attracted the greatest controversy and include disturbance (3, 7), competitive exclusion mediated by shifts in the identity or heterogeneity of limiting resources (8–10), and evolutionary history and dispersal limitation (11).

However, the theoretical justification for a hump-shaped PRR has been challenged (12), and the empirical evidence is mixed. For example, recent meta-analytical syntheses concluded that evidence for a single, canonical pattern was weak (13–15). A large percentage of studies exhibited negative, U-shaped, or nonsignificant PRRs in addition to unimodal and positive linear patterns, and the frequency of these various patterns depended on taxon and spatial scale. Subsequent critiques of the meta-analyses argued that the apparent lack of generality in PRRs might simply reflect methodological inconsistencies among the field studies (16, 17). First, PRR studies vary widely in their choice of both the grain (the area of the sampling unit) and extent (the area over which sampling units are spread) (15, 18). Because of the strong effects of area and heterogeneity on richness, such differences in scale confound cross-study comparisons (19). Second, many of the studies included in PRR meta-analyses did not measure primary production directly but used weakly related surrogates such as latitude, temperature, or altitude (14).

We assessed the generality of the PRR and addressed previous methodological inconsistencies by conducting standardized, observational sampling in 48 herbaceous-dominated plant communities on five continents (Fig. 1 and table S1) (20). We sampled plant species richness in standard 1-m2 quadrats located in blocks of 10 plots, holding grain constant and minimizing differences in extent across sites. In addition, we used the same protocol at all sites for estimating aboveground net primary production (ANPP) as peak-growing-season live biomass, an effective measure of ANPP in herbaceous vegetation (21), especially when consumption by herbivores is low (fig. S1).

Previous work indicated that the form of the PRR might vary with the spatial extent of sampling. Although significant PRRs have been observed at spatial extents ranging from individual

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plots located within one community to means of
sites spread across continents, the hump-shaped
pattern has emerged most frequently in studies
that cross community boundaries (14, 22). PRRs
described within communities may be weaker
because of the potential for limited variation in
productivity among sampling plots as well as
measurement error on individual samples (22)
and because mechanisms involving variation in
species pools and dispersal are excluded. We
tested for scale-dependence by characterizing the
shape of the PRR at three spatial extents: (i) The
within-site extent compares richness and produc-
tivity sampled in individual plots; (ii) the regional
extent compares site-level averages for 1-m² rich-
ness and productivity among sites occurring within
a biogeographic province; and (iii) the global ex-
tent compares site-level averages for richness and
productivity among all sites.

The 48 within-site PRRs took all possible
shapes in parametric regressions of species rich-
ness on productivity (Fig. 2, fig. S2, and tables
S2 and S3). The most common relationship was
nonsignificant (34 sites), 5 sites had a positive
linear pattern, 5 sites had a negative linear pat-
tern, 3 sites were concave-up (U-shape), and
1 site was concave-down (the classical hump
shape). Repeating this analysis with quasipois-
son regression (20) gave similar results (34 non-
significant, 5 positive linear, 6 negative linear,
2 concave-up, and 1 concave-down). We did
not find factors that explained the variation in
the shape of the within-site PRRs. For exam-
ple, if unproductive sites had positive linear
PRRs and highly productive sites had nega-
tive PRRs, then there should be a correlation
between site-level productivity and the slope
of the within-site linear relationship (18). We
found no such pattern (correlation coefficient
\( r = 0.07, df = 46, P = 0.62 \)), nor were sites that
spanned larger ranges in productivity more like-
ly to show significant PRRs. Specifically, the
probability of finding a non-null PRR was un-
related to the range of ANPP within a site (logistic
regression \( P = 0.20 \)).

We tested the regional relationship between
site-level–average species richness (meters⁻²)
and average biomass production in the three
biogeographic provinces of North America in
which we had more than four sites (Fig. 3).
For the 11 Pacific coast sites, located west of
the Cascade/Sierra Mountain ranges and domi-
nated by non-native species (along with one salt

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**Fig. 1.** Locations of the 48 Nutrient Network sites that provided data for this study. Numbers correspond to the “code” column in table S1. Colors and symbols represent the distinct biogeographic regions also shown in Fig. 3 (see Fig. 3 for key).

**Fig. 2.** Within-site relationships between productivity, measured as peak live biomass (dry weight) and species richness. The inset shows the frequencies of relationships that were nonsignificant (NS, thin dashed lines), positive or negative linear (thick dashed lines), and concave-up (+) or -down (−) (solid curves). Statistical results and separate figures for each of the 48 sites are available in table S2 and fig. S1, respectively. The marginal histograms show the frequency of species richness and peak live biomass across all sites.
Fig. 3. Global relationship between mean productivity, measured as peak live biomass (dry weight), and mean species richness (meters$^{-2}$) at each site. White dots indicate managed sites (burned regularly or grazed by domestic livestock) and crosses indicate sites of anthropogenic origin (pastures, old fields, and restored prairies). The solid curve shows the quadratic relationship between productivity and richness with all sites included; the dotted line shows the linear relationship that remains when the anthropogenic sites are removed; and the dashed line shows the 0.95 quantile regression with all sites included. N. Am., North America.

marsh), there was no significant quadratic ($t = -1.0, P = 0.33$) or linear ($t = -0.27, P = 0.79$) effect of productivity on richness. Removing the highly productive salt marsh site did not change this result. Results for the seven Intermountain West sites located between the Cascade/Sierra and Rocky Mountains were similar: Neither the quadratic ($t = 0.52, P = 0.63$) nor linear ($t = 0.14, P = 0.89$) effects of productivity were significant, and removing the one site grazed by domestic livestock did not change this result. For the 13 Central Region grassland sites east of the Rockies and west of the Appalachian Mountains, we did find evidence of a hump shape, with a significant quadratic effect of productivity on richness ($t = -2.35, P = 0.041$). However, when we removed five sites of anthropogenic origin (restored prairies, pastures, or old fields), the quadratic term was no longer significant ($t = -0.177, P = 0.87$), whereas the linear term was significant ($t = 2.5, P = 0.046$).

At the global extent (Fig. 3), the quadratic effect of productivity on richness was significant ($t = -2.39, P = 0.021$). However, this hump-shaped model, which ignored uncertainty in estimates of site means, explained little variation in average species richness (coefficient of determination $R^2 = 0.11$). Furthermore, the pattern was sensitive to land-use history. When we removed nine sites of anthropogenic origin and the one salt marsh, the quadratic effect was no longer significant ($t = -1.36, P = 0.18$), but a positive linear effect was significant ($t = 2.61, P = 0.013$).

An alternative hypothesis states that productivity sets the upper limit on richness, with stochastic forces such as disturbance causing deviations below this limit (3, 23). We tested for a hump-shaped constraint on maximum richness by conducting quantile regressions on our data at within-site and global extents (we did not have sufficient data to address the regional extent). At the within-site extent, results for the 0.95 quantile regressions were similar to our standard regression analysis, with 39 nonsignificant tests, 2 positive linear, 5 negative linear, 1 concave-up, and 1 concave-down pattern (Fig. S2). The use of lower quantiles (0.7, 0.8, 0.9) generated fewer significant PRRs. At the global extent (Fig. 3), the quadratic effect was not significant ($t = -1.63, P = 0.11$); instead, a positive linear trend emerged ($t = 2.19, P = 0.034$). Testing the relationship between mean productivity at a site and maximum richness observed at that site (Fig. S3) produced a similar nonsignificant quadratic effect ($t = -1.50, P = 0.14$) and marginally significant linear effect ($t = 2.01, P = 0.051$).

Overall, we found no consistent, general relationship between productivity and richness of herbaceous-dominated plant communities at the local, regional, or global extent. When we used both standard and quantile regressions, nonsignificant relationships were most common. Although linear or hump-shaped patterns occurred in particular cases, no strong correlates explained these idiosyncrasies. Furthermore, consideration of land-use history and management changed the form of the regional and global scale relationships. Despite using consistent and appropriate data-collection methods, our results show even less support for a general PRR than did previous synthesis efforts based on meta-analysis (13–15), indicating that inadequate or noncomparable data are not the explanation for the lack of a general PRR.

If theory provided a strong prediction for the form of the PRR, then deviations from the expected pattern would be informative. However, ecologists have proposed many competing models that predict every form of the PRR (12). Furthermore, recent work has emphasized that productivity does not have a direct, mechanistic effect on fine-scale species richness, but rather a complex set of interactions links the two variables (5, 24). For example, productivity and richness each respond to the supply rate as well as the stoichiometry of resources (25–27), with variation in these factors leading to different forms of the PRR. In addition, richness may respond more strongly to disturbance, habitat heterogeneity, and biogeographic and assembly history (3, 11, 28–30) than to productivity. Finally, richness is not simply a function of productivity but it may feed back to influence productivity (31). The weak and variable PRRs we found are consistent with these hypotheses.

Rather than investing continued effort in attempting to identify a general PRR, ecologists should focus on more sophisticated approaches already available for investigating the complex, multivariate processes that regulate both productivity and richness (5, 25, 26). Coordinated, global networks represent a research approach that will be invaluable not only for addressing longstanding debates about the generality of empirical patterns but also for testing the underlying mechanisms.

References and Notes
20. Materials and methods are available as supporting material on Science Online.
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African Wild Ungulates Compete with or Facilitate Cattle Depending on Season

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Savannas worldwide are vital for both socioeconomic and biodiversity values. In these ecosystems, management decisions are based on the perception that wildlife and livestock compete for food, yet there are virtually no experimental data to support this assumption. We examined the effects of wild African ungulates on cattle performance, food intake, and diet quality. Wild ungulates depressed cattle food intake and performance during the dry season (competition) but enhanced cattle diet quality and performance during the wet season (facilitation). These results extend our understanding of the context-dependent—competition-facilitation balance, in general, and are critical for better understanding and managing wildlife-livestock coexistence in human-occupied savanna landscapes. 

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